THE MECHANISM OF CONTROLLED GROWTH OF DWARF APPLE TREES *

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Various methods have been used to dwarf apple trees and induce earlier fruiting. Standard varieties are budded or grafted on clonal varieties of dwarfing rootstocks. These dwarfing rootstocks have been used for at least several hundred years in Europe, and in recent years they have been introduced into North America. In this country dwarfing interstocks are often used. This method was described by John Rea in England in 1665 as follows: "I have found out another expedient to help them forward, that is by grafting the Cyen of the Paradise apple in a Crab, or other Apple-Stock, close to the ground, with one graft, and when that is grown to the bigness of a finger, graft thereon about eight inches higher, the fruit desired, which will stop the luxurious growth of the Tree, almost as well as if it had been immediately grafted on the forementioned layers, and will cause the Trees to bear sooner, more and better fruits" (Graves, 1950).

The practice of ringing the bark of fruit trees and vines to induce earlier fruiting is an even older art and was described by Virgil and Columella (Louden, 1850). In 1820 Williams described the effects of girdling grape vines as follows: "At the end of July and the beginning of August, I took annular excisions of bark from the trunks of several of my vines, and that the exposed alburnum might be again covered with new bark by the end of autumn, the removed circles were made rather less than a quarter of an inch in width. In every case in which circles of bark were removed, I invariably found that the fruit not only ripened earlier, but the berries were considerably larger than usual, and more highly flavored". The girdling of grape vines is still a standard practice (Weaver, 1955). The girdling of fruit trees, however, has been largely abandoned.

The practice of training the branches of fruit trees in a horizontal position to suppress growth and induce earlier fruiting has long been practiced in Europe. The knotting of the stems of trees by the Japanese to augment the production of miniature ornamental trees is also an ancient art.

A new technique for dwarfing trees has been developed recently, based upon the polarity of phloem or auxin transport (Sax, 1954). This practice involves the removal of a ring of bark from the trunk of a tree and replacing it in an inverted position. The inverted ring of bark is bound tightly with a rubber band until it is united with the wood. Because of the inverted polarity, the ring of bark acts as a phloem block, inhibiting the flow of plant nutrients to the roots of the tree.

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The physiological mechanism of the dwarfing effect of girdling, of dwarfing rootstocks and interstocks and of bending the branches of a tree was known by Thomas Andrew Knight nearly a hundred and fifty years ago. According to Knight (1822) the nutrient sap elaborated in the leaves passes down the bark, and when checked by girdling the bark, "the repulsion of the descending fluid therefore accounts . . . for the increased produce of blossoms, and the more rapid growth of the fruit upon the decorticated branch. . . ." The effect of the dwarfing rootstock was attributed by Knight (1822) to the obstruction of the descending sap at the graft union. He observed that "the effects produced, both upon the growth and produce of the tree, are similar to those which occur when the descent of sap is impeded by a ligature, or by the destruction of a circle of bark". In 1803 Knight, in discussing the fruiting of horizontal branches, observed that it was "by no means improbable, that the formation of blossoms may, in many instances, arise from the diminished action of the returning system in the horizontal or pendent branch". Thus, all of these mechanisms of dwarfing and induction of earlier fruiting are attributed to the checking of the flow of nutrient sap to the roots, which checks vegetative growth, and the accumulation of the nutrient sap in the top of the tree, which promotes flowering and fruiting.

The advent of radioactive tracers has made possible a more critical analysis of the physiological mechanism of dwarfing trees by bark inversion and dwarfing rootstocks and interstocks. In 1954 a series of experiments were started to trace phloem transport in dwarf apple trees with the aid of radioactive phosphorus.

The radioactive phosphorus was carried in a solution of KH_2PO_4 which had a radioactivity of about 1 mc. per ml. From 0.35 to 1.0 ml. of the solution was poured into a small glas tube which had been sealed at the lower end around the cut petiole of a leaf. One ml. of the solution was absorbed in from 35 to 45 minutes. Tests with a Geiger counter showed that the radioactive phosphorus reached the base of the tree, a distance of 1.5 to 2.0 feet, in from 4 to 6 hours, and that the accumulation of the isotope was well defined in about 3 days.

The first experiment was done on a Baldwin apple tree three years old which had been dwarfed by inverting two rings of bark the previous year. The isotope was fed through the petiole of a leaf on the lowest lateral branch. The speed of transport to the end of the lateral branch indicated that the isotope entered the xylem and passed up the stem in the transpiration stream. After its incorporation in the leaves into the organic nutrients it passed down the phloem. The distribution of the isotope three days after application is shown in figure 1. There was a gradual increase in radioactivity from the lateral branch down the trunk. The counts reached a maximum of 126,000 per minute in the inverted bark. Below the inverted rings of bark the count was greatly reduced to little more than 15,000 counts per minute. Obviously the downward flow of the isotope, and presumably of the organic nutrients was greatly retarded by the inverted rings of bark. As a result there was an accumulation of the isotope

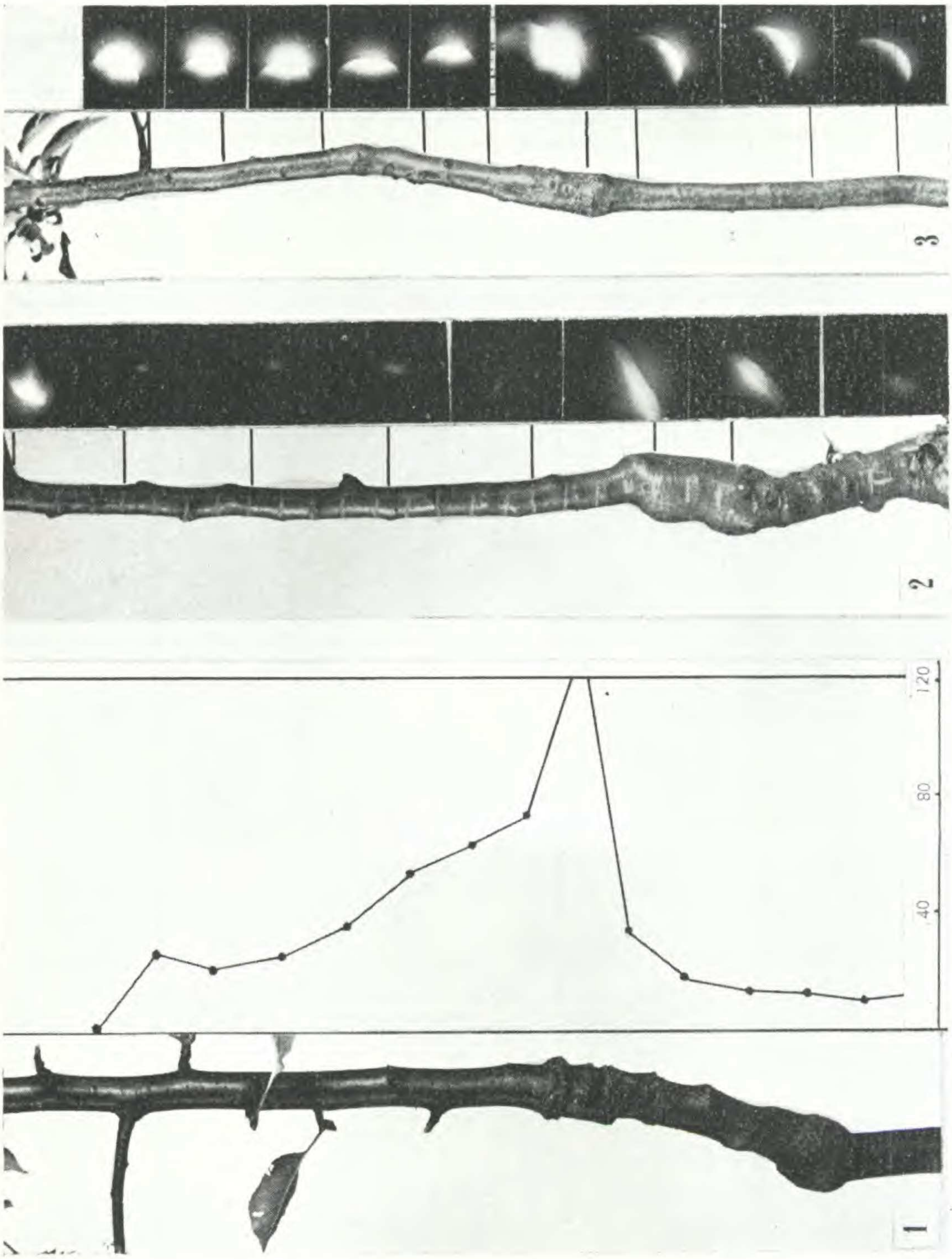

FIG. 1. The distribution of radioactive phosphorus in the trunk of an apple tree, which had been dwarfed by inverting two rings of bark, was measured with a Geiger counter three days after the application of the isotope. Note the great concentration of the isotope at the inverted ring of bark, and the great reduction in concentration below the bark inversion. In all cases the isotope was fed through a leaf petiole on the lowest lateral branch. (Measured in thousands of counts per minute.)

FIG. 2. The distribution of the isotope in the stem of an apple tree on a Malling IX interstock is shown by autoradiographs of transverse stem sections cut three days after the application of the isotope. Note the concentration of the isotope in the dwarfing interstock.

FIG. 3. The distribution of the isotope in the stem of an apple tree with a Clark's Dwarf interstock is shown by autoradiographs of stem sections cut seven days after the application of the isotope. The isotope is concentrated in the dwarfing interstock.

for a considerable distance above the bark inversions and phloem transport to the roots was reduced.

The tracing of the flow of the isotope down the trunks of young apple trees dwarfed by dwarfing interstocks presented a more difficult problem. The dwarfing interstocks have a relatively thick bark and the greater distance between the phloem and the outer surface of the bark reduces the beta radiation reaching the Geiger counter. In order to avoid the discrepancy caused by the differencse in thickness of the bark of the Malling IX and Clark's Dwarf interstocks and the rootstock and scion varieties, the concentration of the isotope was measured by autoradiographs of transverse sections of the trunk of the tree. The trunks of the young trees were cut in transverse sections about 5 mm. thick and numbered serially from top to bottom. Sections from various parts of the stem were mounted on a cellophane sheet and the cellophane was drawn tightly over a glass plate. Ansco isopan film, emulsion side down, was placed on the cellophane and the stem sections were exposed for 15–20 hours. All sections of a tree were exposed, developed and printed together to insure uniformity of treatment.

The isotope was fed into the end of a severed petiole of a five-year-old McIntosh apple tree which had been dwarfed by a Malling IX interstock on a *Malus sikkimensis* rootstock. Three days later, on June 14th, the trunk of the tree was cut into serial sections and autoradiographs of selected sections were made on June 16–17. There was a rather high concentration of the isotope at the junction of the lateral branch with the main trunk of the tree, but only very low concentrations in the lower trunk of the tree above and below the interstock. The Malling IX interstock, however, showed a great concentration of the isotope, as shown in figure 2.

In the third experiment the isotope was fed into a petiole on the lowest lateral branch of a three-year-old Starking apple tree on a Clark Dwarf interstock with a Virginia Crab rootstock. Stem sections were made seven days later and the autoradiographs were made with a 17 hour exposure. The results are shown in figure 3.

The high concentration of the isotope at the junction of the lateral branch with the trunk of the tree was again evident. Considerable radioactivity was found between the junction of the lateral branch and the Clark's Dwarf interstock, followed by a considerable increase in the interstock and a reduction below the interstock. Autoradiographs of four sections through the interstock were obtained and all showed a marked increase in radioactivity with the greatest concentration near the bottom of the interstock. It is evident that both Malling IX and Clark's Dwarf interstocks accumulate the isotope, and presumably the organic nutrients, carried down the phloem.

The fourth experiment was done with a four-year-old McIntosh tree which had been dwarfed by tying a knot in the *M. sargenti* interstock. In 1955 five such trees flowered and fruited heavily while the five adjacent control trees, in which the interstock was not knotted, bore no flowers. The isotope was applied in the usual manner and the stem sectioned three days later. Autoradiographs showed a great concentration of the isotope at the junction of the lateral branch with the main stem, and a secondary and less marked concentration in the stem just above the knot and at the lower end of the knot before the stem began its upward turn. There was little radioactivity in the upper side of the loop or in the stem below the knot. Although the results were not as striking as those obtained with trees dwarfed by bark inversion or dwarfing interstock, there was some indication that the knot had restricted phloem transport.

The dwarfing effect of inverting a ring of bark appears to be caused by the checking of phloem transport, but the mechanism may involve other factors. Since phloem transport is not polar, the inversion of a ring of bark should not interfere with the pressure flow mechanism (Bonner and Galston, 1952). Auxin transport is, however, normally polar and its basipetal movement would be prevented by inverting a ring of bark. Inhibition of auxin flow is indicated by the fact that the dormant buds below the inversion are stimulated into active growth and new growth continues during the summer even when the first sucker branches are removed. Some release of dormancy is effected by simply removing a ring of bark and replacing it in the normal position, but this effect is much more temporary.

The deficiency of auxin in the inverted bark may inhibit phloem transport directly, or indirectly, by the inhibition of cambial activity and growth of the stem. It is known that the inversion of a ring of bark suppresses the growth of the stem in the inverted region, and in a rapidly growing tree there is a great overgrowth of the stem above the inversion.

The dwarfing effect of the dwarfing interstocks also appears to be associated with the retardation of phloem transport. Since the dwarfing interstocks are normally polarized there should be no blocking of the basipetal movement of the auxin. In contrast to the inverted ring of bark the dwarfing interstock grows more rapidly than either the stem of the rootstock or the stem of the scion variety. Perhaps both phloem and auxin transport is retarded in the dwarfing interstock. It may be of some significance that the most effective dwarfing interstocks are varieties which are natural dwarfs when grown on their own roots.

The dwarfing effects of girdling the bark, the use of dwarfing rootstocks and interstocks and the inversion of a ring of bark on the trunk of the tree appear to be associated with the retardation of phloem transport, but dwarfing effects may also be caused by other factors. Peach trees dwarfed by budding them on *Prunus tomentosa* rootstocks show no retardation of the isotope at or below the graft union, nor is there any overgrowth of the dwarfing rootstock as is found with dwarfing Malling apple rootstocks. Even in certain graft combinations of apple varieties the dwarfing effect is not due entirely to the graft union or to the stem of the rootstock (Sax, 1954).

The organic nutrients accumulated at, or above, the phloem block may diffuse into the xylem and be carried by the transpiration stream to the branches where they are used in the production of fruit, as was suggested by Knight in 1820. There is amply experimental evidence to show that nutrient may pass from phloem to xylem or from xylem to phloem (Crafts. 1951). Colwell (1942) found that radioactive phosphorus applied to the leaf will move down the stem to, but not beyond, a deleted ring of bark, and that immediately above the ring the isotope is found in the xylem as well as the phloem. Greene (1937) obtained a higher starch and sugar content of spurs on ringed branches of Grimes Golden apples than was found on the control branches. Leonard (1938) found that the leaves of an apple variety grown on a Malling IX dwarfing rootstock had a higher content of soluble carbohydrates than those of the same variety of apple grown on a standard rootstock. Stanley Burg in 1954 (unpublished data) found that within a week after the inversion of a ring of bark on the trunk of a maple tree the carbohydrate content of the leaves was greatly increased. Thus the phloem blocks not only check the flow of organic nutrients to the roots, but also increase the organic nutrients of the leaves.

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SUMMARY

Apple trees may be dwarfed and induced to fruit earlier by grafting them on a dwarfing rootstock or interstock, or by inverting a ring of bark on the trunk of the tree. The mechanism of these dwarfing effects was

studied with the aid of radioactive tracers. Radioactive tracers were fed through the petioles of the leaves of the lateral branches of young trees. Several days later the distribution of the isotope in the trunk of the tree was determined with a Geiger counter and by autoradiographs of transverse stem sections. The great concentration of the isotope in the dwarfing interstock or in the inverted ring of bark indicates that the dwarfing effect may be caused by checking the flow of organic nutrients to the roots, but the mechanisms involved may be indirect and diverse.